CONE-MONOCHROMATISM

By R. A. WEALE

From the M.R.C. Group for Research in the Physiology of Vision,
Institute of Ophthalmology, London

In the absence of any other clue, a person with monochromatic vision is unable to appreciate differences between hues of equal luminance. His monochromatism is diagnosed by his ability to match any two colours merely by equating their luminances, when all other clues are absent. Two principal types of this defect have been described in the literature. One, rod-monochromatism, is so well known and its characteristics have been so extensively described that most visual physiologists are no longer interested in it. However, the other, cone-monochromatism, has been encountered so rarely that its very existence has been conceded only in pathological cases. The two types differ in their frequency of occurrence and mode of inheritance. Thus rod-monochromatism occurs once in thirty thousand, and many blood relations of one family can exhibit it. The incidence of cone-monochromatism, on the other hand, has been estimated at one in a hundred million (Pitt, 1944a), and has never been noted more than once in a family. The two types differ also by their concomitant symptoms. Cone-monochromatism has none, while rod-monochromats suffer always from reduced visual acuity, and frequently from nystagmus and photophobia. The spectral variation of the rod-monochromatic sensitivity closely agrees with the absorption spectrum of visual purple: this fact, coupled with the central scotoma experienced by rod-monochromats, supports the view that the defect is due to the inactivity or absence of cone-mechanisms. A satisfactory explanation of cone-monochromatism has not been advanced.

Since more detailed information on cone-monochromatism was urgently required because of the light it might shed on theories of colour vision in general, a nation-wide search for cone-monochromats was initiated in June 1950. There is little doubt that the apparent rarity of the defect is partly due to inadequate methods of detection: e.g. the Ishihara Tables are not very reliable in this respect (Weale, 1953). Accordingly, the methods of screening and detecting cone-monochromats were improved.

METHOD

Screening and identification

An opportunity, kindly offered by the Editor of the *Sunday Express*, was accepted by appealing for the co-operation of totally colour-blind persons who fulfilled the following three conditions:

(1) They must confuse coloured photographs with black and white photographs.

(2) They must have good visual acuity.

(3) Light must not cause them any discomfort.

These conditions, on which no compromise was permitted, served to eliminate rod-monochromats since these have reduced visual acuity and are photophobic. Twenty-three people replied, the majority of whom admitted some colour discriminating ability when questioned more closely. Those who lived near London and showed some promise were invited for separate interviews at which the following tests were made. The observer was shown large and small objects of different colours and asked the colour names. The Ishihara Tables were used at reading distance and at about 3 yards. Finally, the observer was asked to match a red (650 mμ) and a green (530 mμ), the green and a blue (460 mμ), and lastly, the red and blue fields on the Wright colorimeter (1946), the bipartite field subtending at the eye an angle of 1° 20'. Failure to make matches led to rejection.

In fact, only one person, A.R.J., aged 34, a man of high intelligence and a capable observer, fulfilled these preliminary tests satisfactorily. His colour naming was not unsystematic but partly governed by luminance. He was incapable of reading any of the Ishihara Tables at reading distance, and at a distance of 3 yards only no. 1. His visual acuity, corrected for a refractive error acquired during an attack of measles, was 6/3.

To test potential observers living outside London, a portable chromatoscope was constructed (Fig. 1). A 3·5V 1W lamp lit by an Ever Ready battery, was placed at the focus of lens L_1. The parallel beam thus formed was divided into two parts by the right-angled prism P, which passed one-half through an Ilford Bright Spectrum filter F_1 and the lens, L_2, forming an image of the filament on the plane steel mirror S. A neutral wedge W made it possible to reduce the intensity of this beam. On its return journey the beam passed again through W and L_2 but missed F_1; it was intercepted by the photometer prism M, one-half of whose diagonal plane was silvered. This reflected the beam, and lens L_3 formed an image of the filament in the plane of the artificial pupil A. A field lens L_4 enabled an emmetropic observer to see lens L_3 in Maxwellian view: a circular aperture D of angular diameter 2° was placed so as to be bisected by the central silver edge of M. The other half of the parallel beam formed by L_1 passed through a neutral density filter and another Ilford Bright Spectrum filter, F_2. This differently coloured light filled the right-hand half of the circular field offered to the observer. The whole optical system was mounted on an aluminium base into which fitted four telescopic supports, enabling one to adjust the height of the instrument on a table without cramping the observer. No mouthpiece was used. If the observer was totally colour-blind then he or she would be able to produce a perfect match between the two halves of the field no matter what their colour, simply by altering the brightness of one of them (the left one in this case). The nature of the test was explained with two neutral density instead of coloured filters in F_1 and F_2 respectively. This enabled the experimenter to check on the observer's reliability. In the presence of the coloured filters (nos. 205, 622, 625) an additional neutral density filter was placed in the right-hand path since the equalization of the two brightnesses might otherwise have been impossible.

Eight of the more promising correspondents who lived outside London were examined with this apparatus and one of them, J.G., a 31-year-old woman, was found to be totally colour-blind and a reliable observer. She could read only no. 1 of the Ishihara Tables at both distances. Her results slightly differed from A.R.J.'s, so that another approach was made to the *Sunday Express*. This led to the discovery of three more totally colour-blind observers: P.S., who could not read any of the Ishihara Tables, but matched any spectral stimulus on the Wright colorimeter with any other, merely by equating their luminances; D.A., who could read some of the tables but was proved to

be totally colour-blind by the chromatoscope test; and A.B. This intelligent young man, aged 18, could also read a number of the tables but satisfied the chromatoscope test and, later, tests on the Wright colorimeter. None of the above showed any of the symptoms of rod-monochromatism. Observers A.R.J., J.G., A.B., and P.S. were tested on the Wright colorimeter. P.S. unfortunately
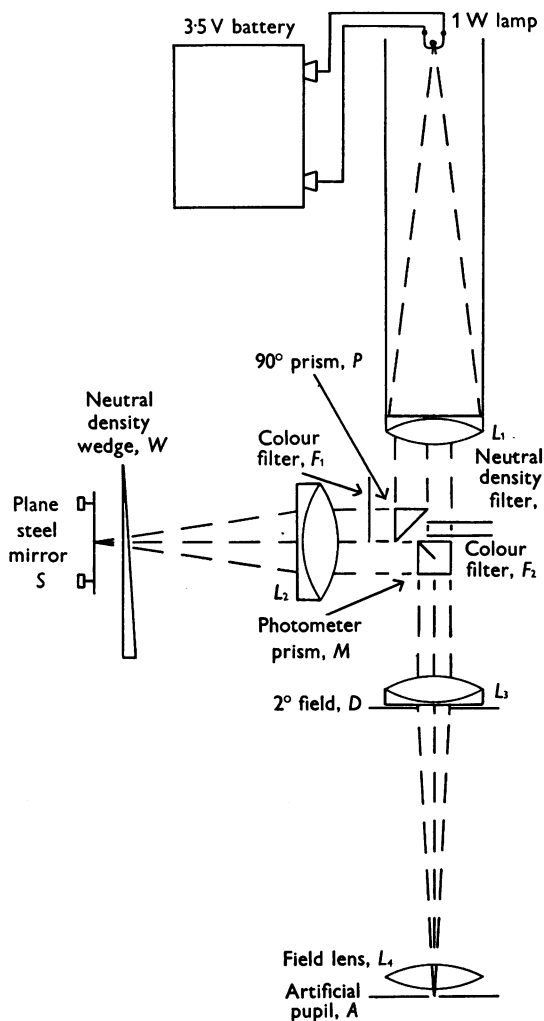

Fig. 1. The chromatoscope (for explanation see text).

emigrated to Canada on the day after the one and only test. Consequently, only the first three could provide comparable data. Before the actual measurements were made these observers were subjected to further searching tests.

Use of colour names. A closer investigation of the observer's colour naming revealed that they were at a complete loss with a 15′ field. A.B.'s use of names was governed by luminance, a fact strikingly borne out by a scale of greys which he had produced to help him in collecting postage stamps. J.G.'s colour descriptions were similar to those which might be employed by a person

unacquainted with colour names: red and orange were 'like the setting sun', a dark blue was 'like the night sky', a blue-green was invariably called 'dirty'. It is interesting to note that if a red colour was matched to green in luminance so that they appeared identical, the whole of the test-field received the 'setting sun' attribute, similarly for the others when matched to green (530 mμ). But when red and blue were matched to each other the answer was uncertain. A.R.J.'s use of colour names was very revealing. Any dark surface was 'blue', any light surface 'yellow' or 'cream'. Red surfaces were usually named correctly because they 'stand out'. He inferred 'green' either because none of the above seemed applicable or because he knew the object to be green. The fact that red 'stands out' is familiar also to people with normal colour vision, and may be due to chromatic stereoscopy. A.R.J., however, found red to 'stand out' also in monocular vision, which suggests that he might be sensitive to chromatic changes of accommodation.* This particular observer was subjected to a colour-naming test in which he was presented with a sheet of white paper (10° × 20°) illuminated with a tungsten filament lamp (40 W 240 V) at a distance of about 2 ft. He viewed it monocularly through Ilford spectrum and neutral density filters in turn presented in a random manner. His responses were as shown in Table 1. He was surprised when told after the test which was the yellow filter: 'I thought yellow was much lighter.' But when the

TABLE 1. Colour names given by A.R.J. to various Ilford bright spectrum and neutral density filters

Test	1st series	2nd series
Neutral (density = 1·0)	Red	Bluish
Green	Blue	Blue
Yellow	Red	Red
Neutral (density = 1·3)	Blue	—
Red	Dark red	Dark red
Blue	Purple or deep blue	Dark blue
Orange	Red	Red
Neutral (density = 2·0)	?	?
Violet	Dark, dark blue	Dark blue
Neutral (density = 1·3)	?	?
Yellow-green	?	?

stimuli were spectral and smaller in area (1° 20'), and there was no additional clue, such as a back-ground illumination to help A.R.J., his colour naming was as shown in Table 2 (col. 1). When the other half of the test-field (530 mμ) was also presented and the two luminances were matched the answers were those shown in col. 2. The difference in the responses to spectral and non-spectral stimuli may be due to the fact that the latter subtended a larger field. A.R.J. was at a loss also with small field non-spectral stimuli. It may well be that his responses to spectral stimuli were more erratic because the Wright colorimeter is fitted with an achromatizing lens in the exit pupil. This lens (Wright, 1946) is so designed as to neutralize the chromatic aberration of the human eye. If A.R.J. receives a clue to colour by the chromatic aberration of his eye and the latter is neutralized, the clue will disappear and his naming become erratic. If a field of 530 mμ is juxta-posed and his eye is out of alinement to but the smallest degree, part of the clue will again be available and his colour naming become more systematic. The tables show that, when presented with fields of adequate size, A.R.J. was able to allot to them fairly applicable colour names, especially when red or blue was involved. Nevertheless, he could match the two latter, although he confused them less frequently than any other (green was called blue or red). It would appear that, in his colour naming, A.R.J. relied on the activity of one or more mechanisms other than those normally mediating the sensation of colour. The chromatic aberration of the dioptric system could provide one of them. But since A.R.J., like the other observers, was able to match any part of the visible spectrum with any other merely by altering the relative luminance, he could be called a cone-monochromat in spite of his use of colour names.

* This has since been confirmed by Fincham (1953).

Further preliminary tests. Before any measurements were made, each of the three observers was asked to match single spectral stimuli, chosen at random, with other single spectral stimuli, also chosen at random. They succeeded in making a match in every case except when the insufficiency of the energy output of the lamp made this impossible at high luminance levels; on reducing the latter, a match became possible once again.

Attempts were made to obtain wavelength discrimination curves with A.R.J. and A.B. in the following manner. The upper and lower fields (*A* and *B*) were both set to $\lambda = 650$ mμ and the observer matched their luminances. He then changed *B* to a shorter wave-length: by adjusting the intensity control of *A* he could then match the luminance of the new wave-length to that of

TABLE 2. Colour names given by A.R.J. to various spectral stimuli, (1) in the absence, (2) in the presence of a juxtaposed field of 530 mμ

	Name	
λ (mμ)	(1)	(2)
420	Blue	—
440	Blue	Red for a moment, then it turned blue
450	Blue	Blue
460	Dark red	—
470	Red or uncertain	Red
490	Blue	—
510	Red	Blue
550	Neither red nor blue (!)	—
600	Uncertain	—
630	Light red	Red
640	Yellow when bright, blue when dark	—
650	Yellow when bright	—
670	Red when dark	—
680	Uncertain	Red
690	Pillar-box red: when very bright it looks like a flame	—

650 mμ. Next he changed *B* to a wave-length shorter than before, and matched the luminances again, and so on till *B* was in the violet. In all cases *A* and *B* were matched in hue. Next, *A* was set to 600 mμ and the procedure repeated. Finally *A* was set to 460 mμ and *B* altered towards longer wave-lengths. Once again, all the matches were performed. In his investigation of tritanopia, Wright (1952) discovered an observer who was nearly totally colour-blind, showing some residual wave-length discrimination in the red at about 630 mμ. To ensure that none of the present observers could be classed with Wright's case particularly close attention was paid to this region in connexion with all three of them: they showed no colour discrimination whatever.

A thorough ophthalmoscopic examination of the fundi of A.R.J.'s eyes, performed by Sir Stewart Duke-Elder, failed to reveal any abnormality. The other observers were not examined.

In cases of this nature, the experimenter depends to a considerable extent on the observers' honesty. Furthermore, Blackwell (1952) has shown that a pay-motive can have some influence on the observer's visual performance. The co-operation of the three observers was motivated by the highest principles, A.R.J. and A.B., in particular, being willing to attend any number of sessions without any regard to reimbursement of expenses.

Numerous tests failed to detect any short-comings in their honesty. For example, if A.R.J. should want to simulate total colour-blindness, why should he think that the first of the Ishihara Tables should be any more legible at a great than at a small distance? Why should he and A.B. find that they can ascribe colour names only to the larger of two equally coloured fields? Did any of the three observers say they could match two stimuli whose intensity was so different that a match was impossible? Tests and traps of this kind revealed beyond any doubt that the answers

these observers gave were honest and their matches genuine. These preliminary tests suggested that A.R.J., J.G. and A.B. conformed with the definition of a cone-monochromat and their photopic spectral sensitivity at the fovea was accordingly measured with 1° 20′ and 15′ bipartite fields in turn.

Measurement of spectral sensitivity

The sensitivity of each observer was measured on the Wright colorimeter (Wright, 1946). The instrument had been calibrated for the purpose of the investigation of tritanopia (Wright, 1952) which proceeded simultaneously with the one on cone-monochromacy. Since a totally colour-blind person does not have to contend with the difficulties of heterochromatic photometry, equating the luminances of the two fields (A and B) is an ideal way of measuring his sensitivity, for it is a null-method. Thus the same criterion can be used in the large and small field measurements, which renders the two sets of data strictly comparable. The wave-length of the field B was set to 530 mμ and kept there throughout the investigation. The wave-lengths of A were chosen in a random order and the observer was asked to match the luminance of A to that of B. The reciprocal of the relative spectral energy giving rise to a sensation of constant brightness at different wave-lengths, and measured at the observer's cornea, represented the spectral sensitivity S_w. The 1° 20′ field was square, A and B forming two equal juxtaposed oblongs, separated vertically. The 15′ field was circular, A and B being divided by a horizontal diameter (cf. Fig. 2).

TABLE 3. Luminance levels and corresponding spectral ranges

	15′		1° 20′	
	Luminance (e.f.c.)	λ (mμ)	Luminance (e.f.c.)	λ (mμ)
A.R.J.	42	510–640	42	490–640
	1·67	460–500, 650–700	1·67	440–480, 650–700
	0·42	420–450	0·42	420–430
J.G.	42	490–630	42	490–630
	1·67	440–480, 640–700	1·67	450–480, 640–700
	0·42	410–430	0·42	410–440
A.B.	42	490–650	42	490–640
	1·67	460–480, 660–700	1·67	450–480, 650–700
	0·42	420–450	0·42	420–440

The usual lack of energy at the extremes of the spectrum made it necessary to reduce the luminance level towards the two extremes of the spectrum. The conditions for each observer are set out in Table 3.

In a single session of 1 hr the whole spectrum was covered once. Since the level of adaptation does not appreciably affect the photopic sensitivity the measurements were not preceded by dark-adaptation, each observer being tested immediately after arrival.

Measurements of the absolute threshold

The absolute threshold was determined for the central fovea by means of a circular 45′ field formed by the prism face of a Hilger monochromator (Weale, 1951), the test wave-length being 530 mμ. A small red light provided a fixation mark at the centre of the field. The fixation light was bright enough to be continuously observable. Two measurements were taken for each observation: (a) the limiting energy at which the test-field did not appear after blinking; and (b) the limiting energy at which it did not disappear a few moments after blinking. The mean of these values is here defined as the absolute foveal threshold. Two observers with normal vision, L.C.T. and R.A.W., also determined this threshold, all the results being referred to the value obtained by the latter.

<div style="text-align: center">RESULTS</div>

<div style="text-align: center">*Spectral sensitivities*</div>

The values have been calculated for an equal quantum spectrum. Figs. 2–4 show the data obtained for A.R.J., J.G. and A.B. respectively. In view of the rarity of these cases the measurements have been collected in Table 4. Each point represents the mean of five independent measurements obtained on
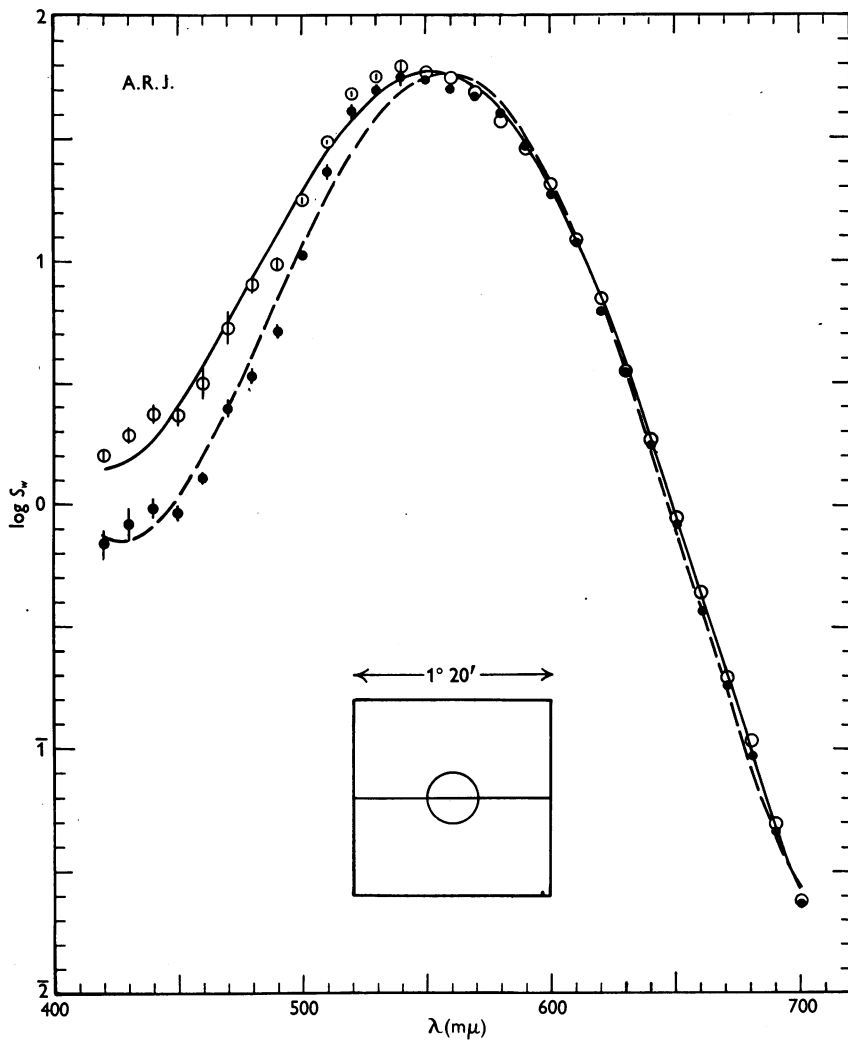

Fig. 2. Foveal spectral sensitivity data. Observer A.R.J. ○ ○ ○, 1° 20′ field; ● ● ●, 15′ field; the relative sizes of the fields are shown. The bars represent $2\sigma_m$.

different days. The mean values of the three large field measurements and those of A.R.J.'s and A.B.'s small field measurements are shown in Fig. 8. The curves in Fig. 2 represent mathematical functions to be discussed below. Apart from the reduction in A.R.J.'s and A.B.'s sensitivity to light of short wave-lengths
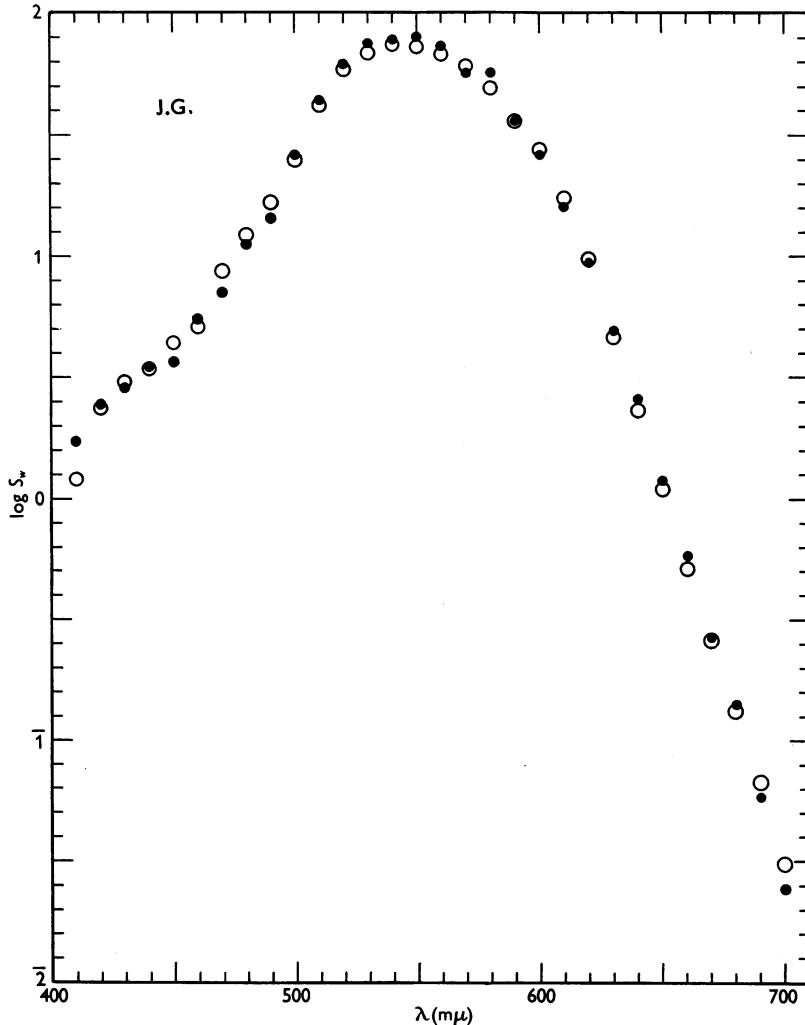

Fig. 3. Observer J.G. (for details see Fig. 2).

with reduction in field size (Figs. 2 and 4), the data for the three observers are substantially similar. Like those obtained for other types of foveal colour vision, they have a single maximum each; it is located at 540–545 mμ. 'Shape-irregularities' occur at 600 mμ, at 470–480 mμ and at 430–440 mμ. In the red, beyond 600 mμ, the trends are smooth.

Some values for the standard errors of the mean are shown in Fig. 2 to indicate the significance of the discrepancy between the values obtained with the small and large fields respectively. The overlapping of the points at longer
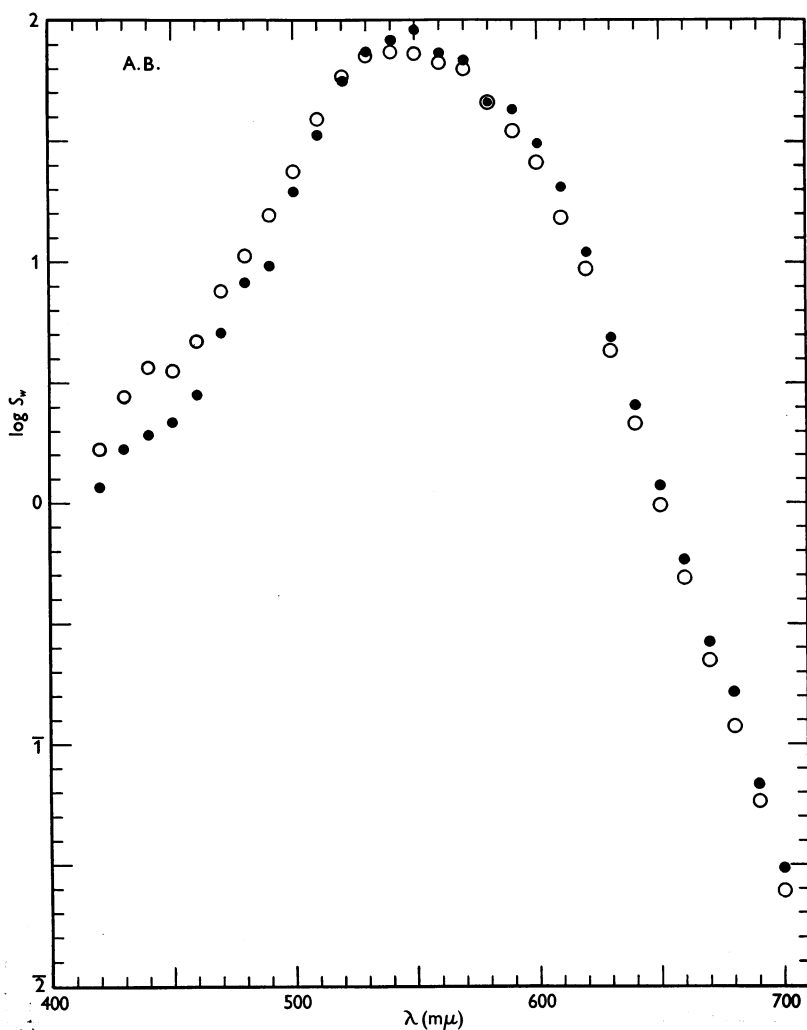

Fig. 4. Observer A.B. (for details see Fig. 2).

wave-lengths would make the vertical bars, representing $\pm \sigma_m$, indistinguishable from each other. The values of σ_m are shown for all three observers in Fig. 5, the larger open circles representing those for the 1° 20′, the small filled ones for the 15′ data. It is interesting to note that J.G.'s values for σ_m at 1° 20′ are erratic, not betraying a systematic spectral variation. A.R.J. and A.B., on the other hand, show distinct deteriorations at wave-lengths shorter

than 500 mμ, which cannot be due only to the reduction in luminance level, because there is no comparable increase in σ_m at longer wave-lengths, and A.R.J. in particular shows an improvement at very short wave-lengths. The σ_m values at 15′ are more erratic for all three observers, tending to a minimum in the green part of the spectrum.

TABLE 4. Values of log S_w for three cone-monochromats

	A.B.		J.G.		A.R.J.	
λ (mμ)	15′	1° 20′	15′	1° 20′	15′	1° 20′
410	—	—	0·238	0·085	—	—
420	0·066	0·226	0·383	0·372	$\bar{1}$·843	0·204
430	0·225	0·451	0·458	0·482	$\bar{1}$·923	0·292
440	0·284	0·564	0·540	0·538	$\bar{1}$·988	0·380
450	0·340	0·552	0·563	0·646	$\bar{1}$·970	0·373
460	0·456	0·677	0·742	0·709	0·120	0·506
470	0·711	0·881	0·848	0·940	0·401	0·736
480	0·919	1·029	1·051	1·088	0·537	0·908
490	0·985	1·195	1·159	1·215	0·723	0·990
500	1·294	1·359	1·413	1·403	1·030	1·252
510	1·524	1·591	1·645	1·626	1·374	1·491
520	1·750	1·762	1·743	1·779	1·614	1·683
530	1·862	1·859	1·877	1·840	1·700	1·754
540	1·918	1·876	1·882	1·878	1·757	1·797
550	1·964	1·864	1·904	1·865	1·745	1·774
560	1·865	1·833	1·864	1·833	1·701	1·757
570	1·838	1·803	1·753	1·784	1·675	1·699
580	1·668	1·669	1·758	1·698	1·607	1·575
590	1·638	1·549	1·564	1·562	1·471	1·462
600	1·494	1·419	1·419	1·441	1·276	1·314
610	1·316	1·184	1·205	1·242	1·075	1·088
620	1·041	0·972	0·978	0·989	0·798	0·845
630	0·689	0·636	0·693	0·664	0·548	0·558
640	0·412	0·335	0·412	0·364	0·247	0·263
650	0·078	$\bar{1}$·991	0·079	0·045	$\bar{1}$·923	$\bar{1}$·946
660	$\bar{1}$·766	$\bar{1}$·689	$\bar{1}$·763	$\bar{1}$·713	$\bar{1}$·566	$\bar{1}$·638
670	$\bar{1}$·424	$\bar{1}$·347	$\bar{1}$·426	$\bar{1}$·417	$\bar{1}$·267	$\bar{1}$·290
680	$\bar{1}$·202	$\bar{1}$·072	$\bar{1}$·148	$\bar{1}$·121	$\bar{2}$·975	$\bar{1}$·031
690	$\bar{2}$·835	$\bar{2}$·762	$\bar{2}$·767	$\bar{2}$·824	$\bar{2}$·667	$\bar{2}$·694
700	$\bar{2}$·483	$\bar{2}$·393	$\bar{2}$·382	$\bar{2}$·485	$\bar{2}$·363	$\bar{2}$·378

Absolute sensitivities

These values related to the 'normal' observer, R.A.W., are shown in Table 5. The sensitivity of A.R.J. is comparable with that of the two normal observers L.C.T. and R.A.W. The two other values are much higher, corresponding to sensitivities 8·8 and 23 times as large as R.A.W.'s.

TABLE 5. Values of the absolute threshold

	A.B.	J.G.	A.R.J.	L.C.T.	R.A.W.
Log S_w for 530 mμ	1·366	0·946	0·191	0·080	0·000

DISCUSSION

Shape irregularities. The most striking feature of Figs. 2–4 is that all the data exhibit shape irregularities in approximately the same spectral regions as those for normal, protanomalous and protanopic observers (Stiles &

Crawford, 1933; Thomson, 1951; Weale, 1951). In order to discover whether or not the data deviate significantly from smooth curves, orthogonal polynomials were fitted to A.R.J.'s results by a method due to Fisher & Yates (1943). The smooth curves in Fig. 2 are of the form:

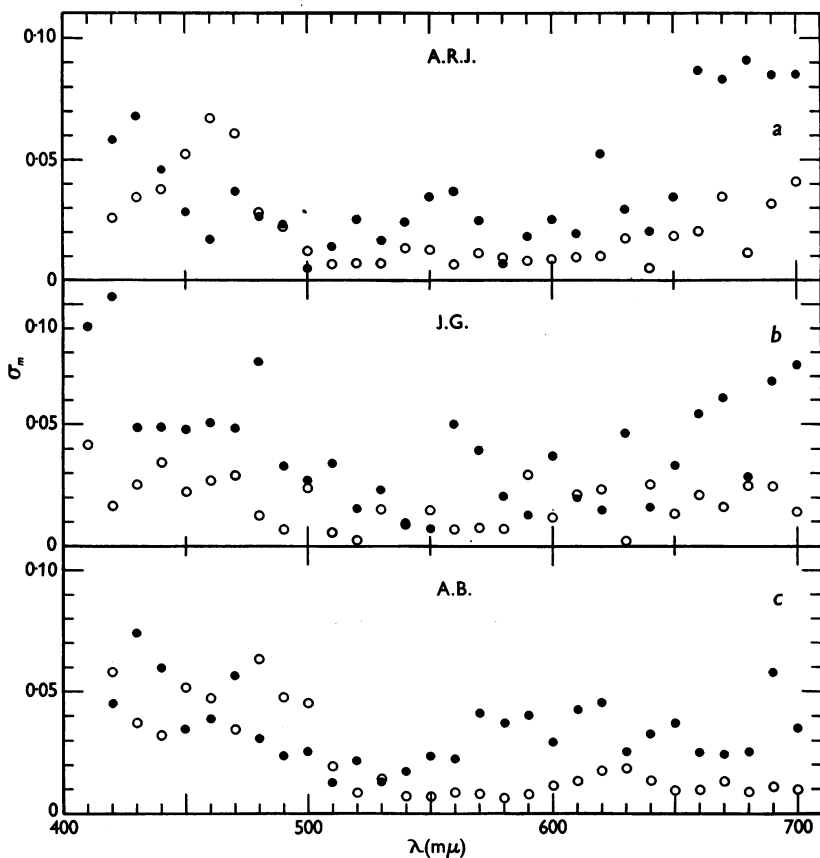$$\log S_w = a + \lambda b + c\lambda^2 + d\lambda^3 + e\lambda^4,$$

Fig. 5. The standard errors of the mean (σ_m) of the sensitivity data (a: A.R.J., b: J.G., c: A.B.). The circles refer to the 1° 20′, the dots to the 15′ data.

where the coefficients of λ are calculated from the experimental data. The question now arises: is the difference between the experimental data and the orthogonal polynomial—which represents the best fitting smooth curve of the fourth order—statistically significant? When these differences are evaluated, and Fisher's z-test is applied to them, they are found to be highly significant even on a 0·1 % basis of probability. The differences (Δ) are plotted as a function of wave-length in Fig. 6c and compared with similar difference curves

obtained for normal (*a*) and protanopic observers (*b*) (Thomson, 1951). It is not without interest that, in general, the differences are maximal at 430 and 520 mμ and that there is a shoulder at 470–480 mμ. Further, the differences obtained for the totally colour-blind observer are similar to the normal,
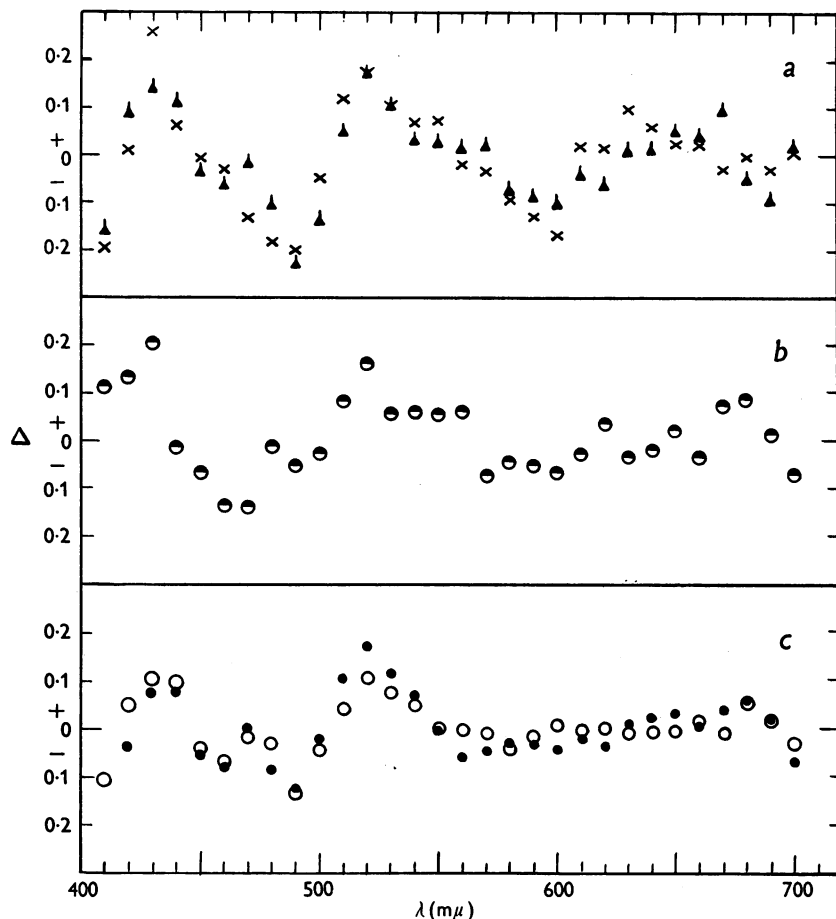

Fig. 6. Values of Δ for two normal (*a*), a protanopic (*b*), and a cone-monochromatic observer, A.R.J. (*c*). ●, 15′; ○, 1° 20′ field.

except in the red part of the spectrum and similar to the protanopic throughout the spectrum. It is even more interesting that a single-humped curve of the fourth order is incapable of doing justice to A.R.J.'s sensitivity curve, thus suggesting that not even a cone-monochromatic sensitivity function is as simple as has been thought in the past (Hartridge, 1949).

The standard errors of the mean. In the wave-length range of 500–700 mμ there is a definite tendency for σ_m to be larger for the 15′ than for the 1° 20′

data. Shown very clearly in connexion with observers A.R.J. and A.B. and, to a smaller extent, with J.G. (Fig. 5), this effect would be expected because of the greater difficulty associated with small field observations. Whereas this tendency persists with J.G. also at short wave-lengths, there is a reversal in A.R.J.'s and A.B.'s data: the large field produces a larger scatter than the small. A.R.J. shows a well-marked maximum at 460 mμ which suggests that this wave-length caused him the greatest difficulty. This was confirmed by information he volunteered. Whereas the shape irregularities in the sensitivity curve may be ascribed to the effect of selective pre-receptoral absorption (v.i.) such an explanation cannot be advanced in order to account for A.R.J.'s and ·A.B.'s σ_m values for the 1° 20′ field. And, as previously noted, the change in luminance levels cannot be made wholly responsible either. Further, if A.R.J.'s and A.B.'s σ_m values for the 15′ field are examined, they reveal a closely parallel course between as large a wave-length range as 420–580 mμ. The trend of J.G.'s σ_m values for 15′ is similar, though the parallel is not so compelling. Crozier (1950) ascribed such reproducible features to 'a property of the excitation process which is not affected by the action of irrelevant absorbers'. He associates them with retinal colour-mediating mechanisms and furnishes evidence in support of this view. If totally colour-defective observers had but a single receptor mechanism governed by the absorption spectrum of a single pigment, such a systematic non-uniform variation of σ_m would be difficult to explain. The tentative conclusion from Fig. 5 is that their defect is post-receptoral.

Comparison of 1° 20′ *and* 15′ *data.* Whereas J.G.'s sensitivity data for the two field sizes are in close agreement with each other, those of A.R.J. and A.B. differ in that reduction in field size decreases the sensitivity to light of short wave-lengths. It will be recalled that the change in field size forms the only variable in this comparison, the method of measurement and luminance levels being the same in both cases except for the small alterations in the spectral range as shown in Table 1. It has been argued that such depressions, also found in some normal observers, may be due to macular pigmentation. The additional postulate required to account for the present depressions is that the macular pigment should be more concentrated at the thinnest part of the retina than anywhere else.

The unreserved acceptance, however, of the suggestion that the depression in the short-wave sensitivity is due only to an increase in the concentration of macular pigment is hardly possible. The reason is that both A.R.J. and A.B. observed structures associated with Maxwell's spot when viewing a 1° 20′ field illuminated by light of wave-length 460–480 mμ. A.R.J. noticed a semi-elliptical dark patch in the upper field when its wave-length was in this region with a corresponding lighter patch in the lower half which was at 530 mμ. Its

appearance is shown in Fig. 7 a. The patch had a major axis of about 20′ and appeared only after a moment's observation, i.e. the eye did not become so adapted as to convey the sensation of uniform illumination. It surrounded the fixation area and was not noticeable when the small field was used. The luminance matches in the 1° 20′ measurements were possible precisely because this 'shadow', as A.R.J. termed it, did not appear till after a moment's observation. It impeded the operation of matching and is undoubtedly responsible for the increased standard errors of the mean at the shorter wave-lengths. It is interesting to note that when the test-field was kept at 460 mμ and the comparison field at 570 and 580 mμ the match was made with greater difficulty than for any other combination.
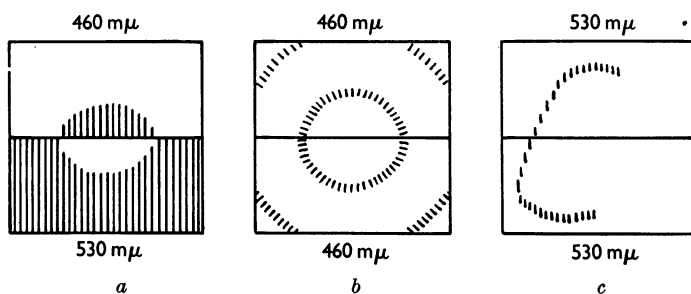

Fig. 7. Entoptic phenomena seen by A.R.J. (*a*), and A.B. (*b* and *c*).

A.B. described the structure shown in Fig. 7 b. By moving the eye vertically and horizontally it was possible to complete the circles which appeared at their best at 460 mμ. Another structure, a dark C shown in Fig. 7 c, appeared within the limits of 517·5 and 601 mμ, being maximal at 524 mμ. This structure surrounded the fixation area and thus caused no embarrassment. Like A.R.J., A.B. had some difficulty with the matches at shorter wave-lengths, a fact which is again illustrated by an increase in the values of the standard errors of the mean for the 1° 20′ field.

J.G. did not observe any of these phenomena. In this connexion it is interesting to note that her 15′ and 1° 20′ data are very nearly the same, and that the spectral variation of her standard errors of the mean for the 1° 20′ field does not resemble the others.

Walls & Mathews (1952) have adduced impressive evidence in favour of the belief that entoptic phenomena, similar to the ones here described, are due to inhomogeneities in the population of receptor-mechanisms. The discovery of such phenomena in totally colour-blind observers might tempt one to the out-right rejection of such a view, and to replace it by a hypothesis which would account for them on the basis of the uneven distribution of the macular pigment. But the refusal of the eye to become adapted to such inhomo-

geneities militates against it. A.R.J.'s and A.B.'s observations suggest that both factors contribute to the reduction of the short-wave sensitivity measured with small fields.

J.G. is obviously in a different class, although her sensitivity data are in excellent agreement with A.R.J.'s and A.B.'s 1° 20' curves. It is a pity that even the simplest type of colour-vision, namely cone-monochromatism, should have to be subdivided.

Comparison between the absolute values of log S_w. Although the agreement in the shapes of the three large field and two small field curves respectively is closer than in most other types of colour vision there are slight but systematic differences in the absolute values. A.R.J.'s data are everywhere somewhat lower than are those of J.G. and A.B. This is unexpected, particularly at 530 mμ since the comparison stimulus was at 530 mμ: if differences might have arisen at all other wave-lengths this one should be excepted. Admittedly, the differences, at 530 mμ are not statistically significant when considered alone, but those at neighbouring wave-lengths are in the same direction. It is possible that one of the observers (A.R.J.) was not perfectly alined—an operation which depends solely on his or her judgement—thus altering the energy content of the comparison field. But a more likely and more plausible explanation lies in a non-uniform retinal distribution of the receptor mechanisms which could lead to such an effect. The absolute values for 530 mμ (cf. Table 4) show that, measured in this manner, A.R.J.'s 15' sensitivity is 32 % lower than the average of J.G. and A.B.'s, and his 1° 20' is 20 % lower than their corresponding average at this wave-length.

The absolute thresholds. Table 5 shows that, of the three cone-monochromats, only A.R.J. had an absolute threshold at all comparable with the ones measured in the colour-normal observers, L.C.T. and R.A.W. The thresholds of J.G. and A.B. were much lower, and this may well be due to temporary inability to fixate: J.G.'s threshold was measured immediately after her arrival from Birmingham, and A.B.'s after a night journey from Glasgow. Both these observers may thus have suffered from train nystagmus which might have impeded the precise fixation required in these measurements of the absolute threshold. Such inability to fixate would lead to the stimulation of some rods with a resultant increase in sensitivity. Perhaps it should be emphasized that this stricture did not apply to the spectral measurements: all the observers were well rested and able to fixate.

Comparison with other monochromats. Abney (1913) gives data for a cone-monochromat, which cannot, however, be compared directly with the present set because his spectrum was not corrected for the inequality of the spectral energy distribution. In order to do this, his photopic curve was divided by the c.i.e. curve. The test determining whether this correction was appropriate

consisted in applying the correction factors thus obtained to Abney's scotopic curve. The new curve was in satisfactory agreement with the scotopic data given by Stiles & Smith (1944), and it was concluded that the correction could
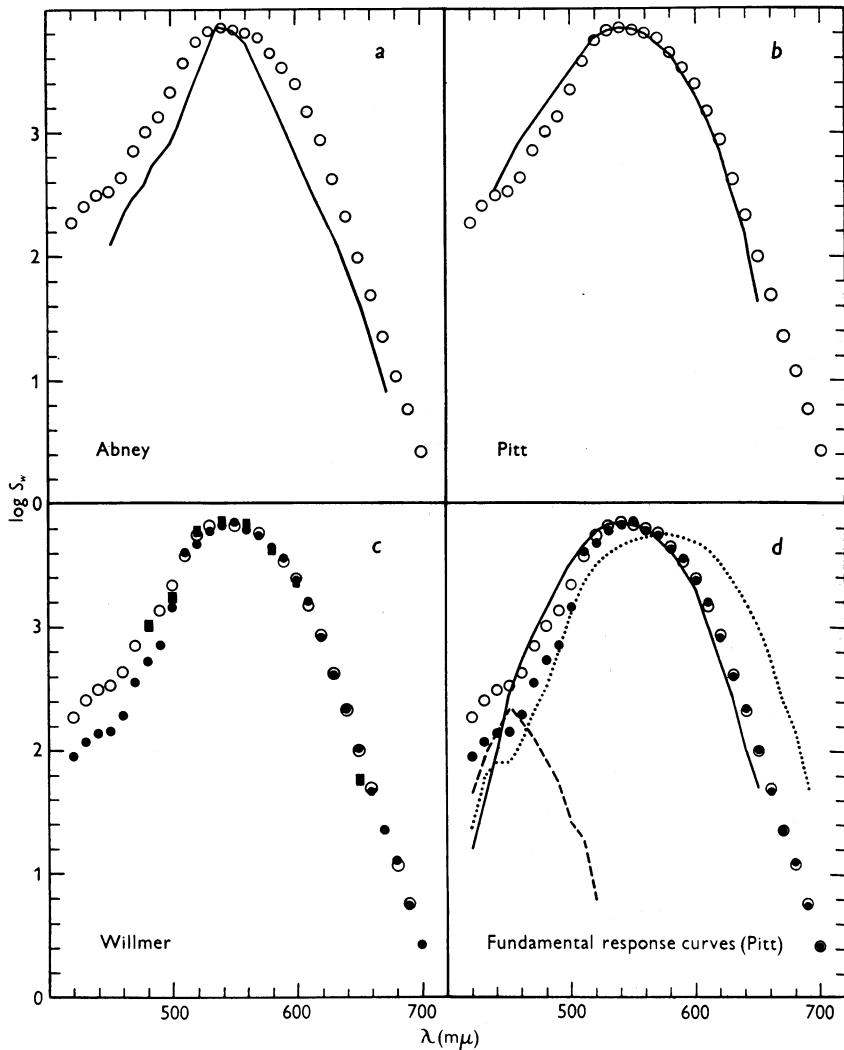

Fig. 8. Comparison of the mean of the 1° 20′ data with Abney's cone-monochromat (a) and with Pitt's cone-monochromat (b); and of both the 1° 20′ and 15′ data with Willmer's results obtained for the central fovea of dichromats (c) and with Pitt's fundamental response curves (d). ○, 1° 20′ field; ●, 15′ field.

be applied to Abney's data for the cone-monochromat. The corrected curve is shown in Fig. 8a, where it is compared with the mean of the present three

1° 20′ data. Except for the location of the wave-length of maximum sensitivity, the correlation is disappointing.

The present data are also compared with those of Pitt's observer (1944*a*), Fig. 8*b*. The agreement between the two is much better in this case than in the other. Part of the remaining discrepancy can be ascribed to the 'smoothing' of the older data, and to the conversion from a percentage to a log basis.

Fig. 8*c* shows a comparison between some of Willmer's (1949) and the present large and small field data. Willmer argued that since the fovea of the normal eye exhibits dichromatic characteristics when tested with very small fields the dichromatic eye might be monochromatic under the same conditions. This expectation was indeed fulfilled, and the oblong points show the protanopic sensitivity curve as measured with a 10′ field: they are consistent with the new values. In view of the finding that a change in field size does not affect J.G.'s sensitivity it is not surprising that Willmer's data do not agree precisely with one set or the other.

A few other cases of cone-monochromatism are mentioned in the literature (cf. Heinsius, 1938; Sloan, 1946, 1951, etc.). None of the authors has, however, measured the observer's spectral sensitivity, or if they have (Sloan & Newhall, 1942) their data are too inadequate to permit a valid comparison; but they are compatible with the present data. The dark-adaptation curve given by Sloan (1946), however, shows the two branches usually associated with cones and rods respectively, thus supporting the view that the defect of total colour-blindness is post-receptoral.

Comparison with Pitt's fundamental response curves. Pitt derived a set of fundamental response curves (1944*b*) by assuming (*a*) that the protanope lacked the long-wave receptor mechanism, postulated by the tristimulus theory, and (*b*) that, in the deuteranope, this mechanism was fused with the medium wave-length mechanism. On the basis of the classical trichromatic theory, the sensitivity of cone-monochromats might be expected to agree with one of the three response curves. Although Fig. 8*d* shows that the 'green' curve is the most promising candidate, agreement between this and either of the cone-monochromatic sets cannot be said to be very good. While the discrepancy at short wave-lengths may be due to Pitt's use of the C.I.E. sensitivity curve, which has recently been shown to be too low in this region (Thomson, 1949; Ishak, 1952), the lack of agreement at longer wave-lengths cannot be similarly explained. It suggests that the cone-monochromatic sensitivity is not really identifiable with Pitt's green fundamental response.

Comparison with other types of sensitivity curve. The view that cone-monochromatism is a defect in its own right and unlikely to be due to a combination of simple factors is reinforced by a comparison between the 1° 20′ data and others obtained for 6 protanopes, 6 deuteranopes (Pitt, 1935), 7 tritanopes

(Wright, 1952), and 2 normals (Thomson, 1949). Their maxima were put equal to 2·000 and plotted in Fig. 9. The protanopes confuse red with green and are characterized by a very low sensitivity to light of long wave-lengths. The
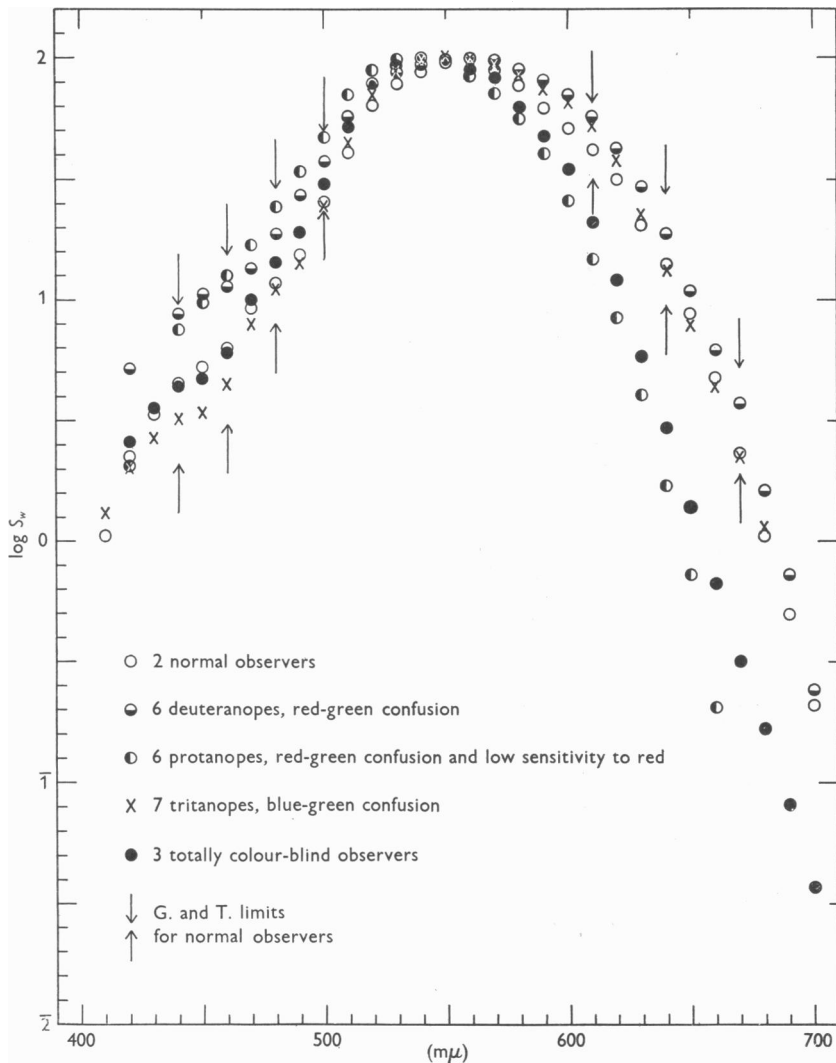

Fig. 9. Comparison of the spectral foveal sensitivity curves characteristic of the five principal types of colour vision.

deuteranopes also confuse red with green but their sensitivity to light of long wave-lengths is nearly normal. The tritanopes confuse blue with green. Fig. 9 thus represents a comparison of all the principal types of colour vision.

Furthermore, the arrows indicate the upper and lower limits which Gibson & Tyndall found for normal observers (1923).

The comparison of these five sets of data reveals a striking fact: if Gibson & Tyndall's limits for normal observers are accepted, there can be, broadly speaking, only two types of sensitivity curve as measured with medium size fields. Cone-monochromats are not characterized by a sensitivity lower than that of other types throughout the whole range of the 'visible' spectrum. Thus there are normal observers whose sensitivity to light of short waves can be much lower than the cone-monochromatic. At the other extreme of the spectrum, the protanopic is systematically lower than the cone-monochromatic sensitivity. It follows that there is not the close correlation between colour vision and spectral sensitivity which has been postulated in the past: vast though the differences between the various types of colour vision may be, the actual spectral sensitivity curves are substantially alike. This is hardly compatible with the trichromatic theory which postulates that the spectral sensitivity is the sum of the three colour-mediating mechanisms.

The general similarity of all foveal photopic sensitivity curves, modified only by a single subdivision, and coupled with the fact that a change in field size can alter the cone-monochromatic sensitivity without a concomitant change in colour vision suggests that the deficiencies in the colour-mediating mechanisms take place, at least in the cone-monochromat, at a level higher than the receptoral. The actual absorption of light seems to take place in all observers by mechanisms which are fundamentally similar: this confirms the view that some colour-defects are of a post-receptoral nature.

Comparison with the absorption spectra of visual pigments. It has been suggested in the past (Abney, 1913; Hartridge, 1949) that the photopic spectral sensitivity of the cone-monochromat corresponds to that of the 'green' cone-mechanism. It would follow that, if this is the only one to function in a cone-monochromatic retina, its sensitivity might be comparable with the absorption spectrum of the responsible cone-pigment, much as the human scotopic curve has been compared with the absorption characteristics of visual pigment 502 (frog visual purple) or the scotopic sensitivity of the tench with those of visual pigment 533 (visual violet). Dartnall (1952) found that the shapes of the absorption spectra of all the known visual pigments were identical if plotted on a frequency abscissa. If, therefore, the cone-monochromatic photopic function were due to the absorption of light by a single pigment, one would expect it to fit the common pattern. The two types of cone-monochromatic sensitivity were corrected for the absorption of light by the ocular media (Ludvigh & McCarthy, 1938), and various amounts of macular pigment assumed in order to obtain empirical agreement. This led invariably to over or under corrections in other spectral regions for which the sensitivity was

calculated. Moreover, at longer wave-lengths the selective absorption by pre-receptoral media is universally thought to be negligble. But not even the long wave-length part of the cone-monochromatic sensitivity function can be made to tally with the pattern if it is assumed to depend on a single pigment. It follows that either Dartnall's pattern does not fit the human 'green' cone-pigment, just as it fails with other photopic dominator and modulator curves, or else the cone-monochromatic sensitivity is not due to a single pigment. Other possibilities hardly arise: e.g. one cannot argue that the disagreement is due to this sensitivity not being scotopic, because pigments 467 (tench), 510 (bleak) and 565 (chick) which fit the pattern are apparently not scotopic either.
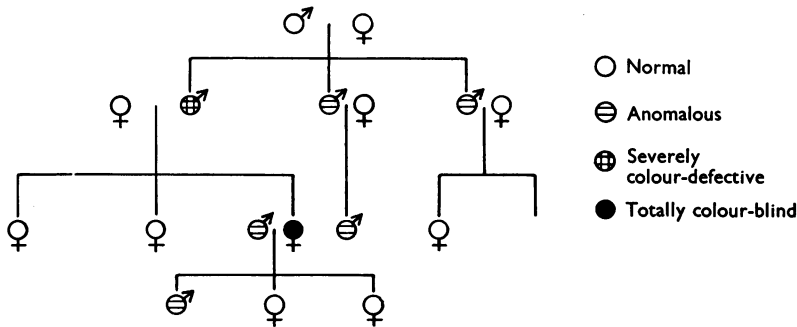
O Normal

⊖ Anomalous

⊕ Severely colour-defective

● Totally colour-blind

Fig. 10. J.G.'s family tree.

Colour vision in the observers' blood relations. The most extensive inquiries have failed to discover any relation of A.R.J.'s who would admit to being colour-blind. A.R.J.'s parents and sister were tested, but found to be normal. Like A.R.J., A.B. had no colour-defective relatives. P.S. had a brother, now deceased, who suffered from a colour defect, and a maternal cousin of his is also colour-defective: no further details could be elicited. J.G.'s father is severely protanomalous (Fig. 10); her mother's colour-vision seems normal although she mis-read Ishihara's Plate 4 (20 instead of 70 or 29). J.G.'s paternal grand-parents are both normal; but two paternal uncles and the son of one of them are anomalous. J.G.'s son (aged 8) was tested and seems to be deuterano-malous: J.G.'s husband, however, is also colour-defective and consequently no deduction can be made from this finding.

The incidence of cone-monochromatism. Pitt's estimate (1944a) of the occurrence of this defect (1 in 10^8) is based on the assumption that it is due to the combination of protanopia and tritanopia. In the light of the above comparison between various sensitivity curves, it is uncertain whether this view can be upheld; but, in any case, Wright's more recent estimate of the incidence of tritanopia as lying between 1 in 12,000 and 1 in 60,000 would increase Pitt's

estimate to 1 in 10^6 or 10^7. It is improbable that the present inquiry elicited replies from all the congenital cone-monochromats in Great Britain; nevertheless, five have been identified so that the corrected value of Pitt's estimate is feasible. The implication is that the frequency of occurrence of cone-monochromatism is governed by that of protanopia and tritanopia respectively, i.e. two separate chromosomes are involved in its inheritance. It would appear, however, that the resultant defect cannot be expressed in terms of the two defects characteristic of these genes respectively.

SUMMARY

1. An account is given of the methods of screening employed in the detection of persons who are thought to be cone-monochromats.

2. Their colour naming is described.

3. The foveal spectral sensitivity of three cone-monochromats was measured between 420 and 700 mμ. Two field sizes, subtending at the eye angles of 15' and 1° 20' respectively were employed. The method consisted in matching the luminance of various spectral stimuli to a constant stimulus at 530 mμ.

4. In two observers there was a significant variation in sensitivity with field size: the sensitivity to light of short wave-lengths was reduced by 50% when the field size was 15'.

5. A wide variation was observed in absolute thresholds measured at 530 mμ: the threshold of one of the observers agreed substantially with those of two colour-normal observers, the two others were much lower.

6. The significance of the data is discussed. They are compared with other data on cone-monochromatism and with Pitt's fundamental response curves. It is suggested that the cone-monochromatic sensitivity cannot be identified with the green response.

7. A comparison of the sensitivity curves, characteristic of the five principal types of foveal colour-vision, is made, and it is suggested that there is conclusive evidence for the existence of only two types of curve. Colour defects are, therefore, thought to be located mainly in post-receptoral structures.

REFERENCES

ABNEY, W. (1913). *Researches in Colour Vision and the Trichromatic Theory*. London: Longmans, Green and Co.

BLACKWELL, H. R. (1952). Studies of psychophysical methods for measuring visual thresholds. *J. opt. Soc. Amer.* **42**, 606–616.

CROZIER, W. J. (1950). On the visibility of radiation at the human fovea. *J. gen. Physiol.* **34**, 87–136.

DARTNALL, H. J. A. (1952). Visual pigment 467, a photosensitive pigment present in tench retinae. *J. Physiol.* **116**, 257–289.

FINCHAM, E. F. (1953). The effect of colour deficiency on the accommodation reflex. *J. Physiol.* **121**, 570–580.

FISHER, R. A. & YATES, F. (1943). *Statistical Tables*, 2nd ed. London: Oliver and Boyd.

GIBSON, K. S. & TYNDALL, E. P. T. (1923). Visibility of radiant energy. *Sci. Pap. U.S. Bur. Stand.* **19**, 131–191.

HARTRIDGE, H. (1949). *Recent Advances in the Physiology of Vision*. London, Churchill.

HEINSIUS, E. (1938). Die 'einfache, unkomplizierte' Form der angeborenen totalen Farbenblindheit. *Klin. Mbl. Augenheilk.* **101**, 489–494.

ISHAK, J. G. (1952). The photopic luminosity curve for a group of fifteen Egyptian trichromats. *J. opt. Soc. Amer.* **42**, 529–534.

LUDVIGH, E. & McCARTHY, E. F. (1938). Absorption of visible light by the refractive media of the human eye. *Arch. Ophthal., N.Y.*, **20**, 37–51.

PITT, F. H. G. (1935). Characteristics of dichromatic vision. *Rep. med. Res. Coun., Lond.*, No. 14, pp. 1–58.

PITT, F. H. G. (1944a). Monochromatism. *Nature, Lond.*, **154**, 466–468.

PITT, F. H. G. (1944b). The nature of normal trichromatic and dichromatic vision. *Proc. Roy. Soc.* B, **132**, 101–117.

SLOAN, L. L. & NEWHALL, S. M. (1942). Comparison of cases of atypical and typical achromatopsia. *Amer. J. Ophthal.* **25**, 945–961.

SLOAN, L. L. (1946). A case of atypical achromatopsia. *Amer. J. Ophthal.* **29**, 290–294.

SLOAN, L. L. (1951). Congenital achromatopsia. *J. opt. Soc. Amer.* **41**, 287.

STILES, W. S. & CRAWFORD, B. H. (1933). The liminal brightness increment as a function of wavelength for different conditions of the foveal and para-foveal retina. *Proc. Roy. Soc.* B, **113**, 496–530.

STILES, W. S. & SMITH, F. (1944). A mean scotopic visibility curve. *Proc. phys. Soc. Lond.* **56**, 251–255.

THOMSON, L. C. (1949). Shape irregularities in the equal energy luminosity curve. *Proc. phys. Soc. Lond.* B, **62**, 787–792.

THOMSON, L. C. (1951). The spectral sensitivity of the central fovea. *J. Physiol.* **112**, 114–132.

WALLS, G. L. & MATHEWS, R. W. (1952). New means of studying colour blindness and normal foveal colour vision. *Univ. Calif. Publ. Psychol.* **7**, 1–172.

WEALE, R. A. (1951). The foveal and para-central spectral sensitivities in man. *J. Physiol.* **114**, 435–446.

WEALE, R. A. (1953). A comparison of the 9th and 10th editions of the Ishihara Tables. *Brit. med. J.* i, 1148.

WILLMER, E. N. (1949). Further observations on the properties of the central fovea in colour-blind and normal subjects. *J. Physiol.* **110**, 422–446.

WRIGHT, W. D. (1946). *Researches on Normal and Defective Colour Vision*. London: Henry Kimpton.

WRIGHT, W. D. (1952). The characteristics of tritanopia. *J. opt. Soc. Amer.* **42**, 509–521.